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PALEOECOLOGY OF *DUNKLEOSTEUS TERRELLI* (PLACODERMI: ARTHRODIRA)

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ABSTRACT

The Cleveland Member (Late Famennian) fish fauna represents one of the most speciose and well-collected faunas from the Late Devonian; however, our understanding of the fauna's paleoecology is limited. Published interpretations of placoderm paleoecology typically suggest that most species are obligate bottom-living forms or are tied closely to life on the bottom. *Dunkleosteus terrelli* (Newberry, 1873) (Placodermi, Arthrodira), however, was a pelagic organism. This interpretation is based on an analysis of the nature of the distal Appalachian Basin depositional habitat and the distribution of this species' remains within the basin. The species presence as fossils represents the remains of organisms that lived within the water column in the basin rather than an allochthonous accumulation of floating carcasses. Thus, the disarticulation seen in specimens of *Dunkleosteus terrelli* is a result of local post-mortem flotation and possible scavenging within the water column. This hypothesis is supported by a Chi-squared statistical analysis for the geographic distribution of *Dunkleosteus terrelli* fossil remains. Finally, estimates of dry and wet weights for *Dunkleosteus terrelli* suggest (1) an inability to rest on the bottom given the physical properties of the sediments and (2) the presence of a mechanism for static buoyancy, which would account for post-mortem flotation in a basin with published estimated depths of 30 to 100 meters.

Introduction

Our understanding of the paleoecology of Late Devonian fish faunas is limited by the lack of high diversity faunas available for analysis. The Cleveland Member (Late Famennian) fauna is one of the best known, possessing 66 species (Hlavin, 1976; Denison, 1979; Williams, 1990; Carr, 1996; Carr and Jackson, 2010) consisting of sharks (33), placoderms (28), and osteichthyans (5).

Paleoecological interpretations of the fauna historically were based on analogy to putatively similar taxa from other faunas. *Coccosteus* (Miles and Westoll, 1968), for example, is often used as an analogue to interpret other arthrodires (e.g., Heintz, 1932, p. 202, used the form of *Coccosteus* to interpret "*Dinichthys*" or *Dunkleosteus*, a comparison across subordinal-level distinct taxa). These analogies often involve the comparison of taxa from dissimilar facies and faunal compositions.

Hlavin (1976) reviewed sedimentological-depositional models to interpret the Catskill Delta and the distal black shales (the Cleveland Member of the Ohio Shale along with other regional shales and their biostratigraphic relationships) and provided an up-to-date faunal analysis for the Cleveland Member. However, he did not consider the impact of sedimentological interpretations on the potential lifestyles of the fishes associated with the depositional habitat of the Cleveland Member.

Williams (1990) provided the first comprehensive predator-prey analysis of the Cleveland Member fish fauna. His analysis

centered on chondrichthyans due to their unusually complete preservation including stomach contents (53 specimens reported with identifiable gastric contents, Williams, 1990, p. 280). Evaluation of non-chondrichthyans was limited to a few cases of associated remains possibly suggesting predator-prey relationships (the presence of a shark spine imbedded in the oral region of an arthrodire; associated arthrodire and shark remains suggesting a possible predator-prey interaction; and a palaeoniscid with shark and arthrodire stomach contents; Williams, 1990, p. 286–287).

Despite the vast amount of effort dedicated to the sedimentological history of the Appalachian Basin (e.g., Woodrow and Sevon, 1985) and the long history of vertebrate paleontology in the region, little work has addressed the paleoecology of the vertebrate fauna associated with these sediments. The placoderms, which represent the most speciose Devonian clade (Carr, 1995) and numerically the largest part of regional collections, represent the least known clade in terms of their paleoecology.

As seen in the examples above, estimates concerning the paleoecology of Paleozoic fishes are based on evidence such as stomach contents, body form, or indirectly on facies analyses. Little is known concerning placoderm stomach contents, although Dennis and Miles (1981) and Miles and Westoll (1968, p. 462) have evaluated stomach contents in *Incisoscutum* and *Coccosteus*, respectively. The interpretation of gnathal-plate morphology is

used to suggest specializations for various feeding strategies such as durophagy or piscivory (Denison, 1978, p. 17). However, the feeding strategies of generalized forms or forms without recent analogues are difficult, if not impossible, to interpret without additional supporting evidence.

Lindsey (1978) and Webb (1982) used body form to interpret locomotor styles among extant fishes. Among placoderms this approach has found limited application being applied primarily to laterally and dorsoventrally compressed forms. Miles (1969, p. 129; see also Moy-Thomas and Miles, 1971, p. 175) suggested a nektonic lifestyle for the laterally compressed brachydeirid arthrodiroids, while several authors (Stensiö, 1963, p. 13; Miles, 1969, p. 129; Moy-Thomas and Miles, 1971, p. 185, 197–198) interpreted dorsoventrally compressed forms, such as the raylike rhenanids, as bottom living. Between these extremes, a vast number of taxa are interpreted generally as bottom living (Stensiö, 1963, p. 13) or specialized for “life just above the bottom” (Moy-Thomas and Miles, 1971, p. 197).

Finally, analysis of the facies in which placoderm fossils are found has provided an additional source of information, but relies on the assumption that fishes lived in a habitat on or above the accumulating sediments. The utility of this approach is difficult to evaluate when post-mortem transport is involved and the fishes lived outside the area of deposition.

Of the methods that have been used to determine aspects of placoderm paleoecology, none individually can provide a complete picture, and thus far, few attempts have been made to combine analyses. Ideal preservation, having complete organisms preserved with soft tissue and stomach contents, is an exceedingly rare occurrence. Within the Devonian, this ideal is achieved among the chondrichthyan remains found in carbonate concretions from the Cleveland Member (Williams, 1990). For placoderms, researchers have retrieved some of the best-preserved fossil material from the Hunsrückschiefer of Germany (Lower Emsian) and the acid-prepared concretions from the Gogo Formation of Western Australia (Frasnian). Even in these conservation Lagerstätten (*sensu* Seilacher, 1990) information is lost. However, a total-evidence approach including, e.g., sedimentology, geochemistry, and taphonomic mechanisms, may recover sufficient information to reconstruct details of life history and paleoecology (Tasch, 1965; Elder and Smith, 1988).

The Catskill Delta and its associated foreland basin (Appalachian Basin, Figure 1C) provide a unique opportunity to analyze the paleoecology of fishes in the region. The black-shale facies found within the distal basin (Figure 1D) represent an anoxic depositional environment, potentially inhospitable to benthic organisms or capable only of supporting a low-diversity fauna (see Discussion below). Fossil fishes found in these shales represent either fishes living and dying within the region, post-mortem allochthonous accumulations of floating carcasses, or a mixture (Brett and Baird, 1993, p. 254).

Historically, most placoderms have been seen as obligate benthic organisms, which accessed the water column only to feed (Stensiö, 1963, p. 13; Moy-Thomas and Miles, 1971, p. 197; Denison, 1978, p. 17), suggesting that the presence of carcasses within the low-diversity deep basin represents an accumulation of remains originating in the established benthic communities of the aerated shallow regions of the basin. To evaluate this hypothesis in one species, the current study analyses the distribution of gnathal elements from *Dunkleosteus terrelli* (Newberry, 1873) within the Appalachian Basin. *Dunkleosteus terrelli* (Figure 2A–C) is a large arthrodire (4.5–6 m in length) found within the

Appalachian Basin. This species is oval in cross-section and possesses a well-developed dermal skeleton (Figure 2B, C) with individual bones up to 5–7.5 cm thick along the lateral and occipital thickenings of the head shield. The gnathal elements (IG, ASG, PSG, Figure 2B, C) in this species represent bones that detach relatively early in the disarticulation process (see Schäfer, 1972, p. 49–91, and Elder, 1985, for a discussion of disarticulation patterns) and would be expected to accumulate close to the site of death (secondary transport after these remains settle is discussed below). The geographic distribution of the gnathal elements for *Dunkleosteus terrelli* does not support a hypothesis where remains of this arthrodire represent long-distance floating of carcasses.

Methods and Materials

Dunkleosteus terrelli specimens from the Cleveland Member (Upper Famennian: *postera* to late *expansa*–early *praesulcata* conodont zones, Zagger, 1995) of the Ohio Shale analyzed in this study are housed within the collections of the Cleveland Museum of Natural History. Data were retrieved from the Museum vertebrate paleontology catalog using those specimens with entries providing detailed locality information. The presence or absence of individual plates indicated in the catalog was confirmed from the actual specimens. The specimen localities included seven north-south river or creek basins and the excavation site for Interstate-71 in northern Ohio near Cleveland (Figure 3). These localities were grouped into five drainage systems representing five north-south transects in northern Ohio paralleling the ancient Catskill shoreline (from west-to-east: 1, Huron and Vermillion Rivers and Chance Creek; 2, Beaver Creek; 3, Black River; 4, Rocky River; 5, Big Creek and Interstate-71). These drainage basins expose the black shales (Cleveland Member) of the distal foreland basin. Recorded specimens included those with and without gnathal elements and isolated gnathal elements. The relative abundance of specimens with and without gnathal elements was evaluated for the localities listed above.

A Chi-squared nonparametric analysis for k independent samples (Equation 1; Siegel and Castellan, 1988) was conducted to test the null hypothesis (H_0) that the proportion of specimens with and without gnathal elements was statistically the same in each geographic sample (i.e., there was no geographic trend and the distribution of fossils was random). The research hypothesis, based on published interpretations of placoderm paleoecology (e.g., Stensiö, 1963; Denison, 1978), was that the proportions differ across samples (an increased concentration of gnathal elements shoreward, suggesting an allochthonous accumulation of fossils within the distal basin from an eastward shallower source). A significance level of $\alpha = 0.05$ was chosen with a sample size of $n = 199$.

$$X^2 = \sum_{i=1}^r \sum_{j=1}^k \frac{n_{ij}^2}{E_{ij}} - N \quad (1)$$

E_{ij} = number of expected cases in the i th row of the j th column when the null hypothesis is true

i = variables within the $r \times k$ contingency table

j = groups within the $r \times k$ contingency table

n_{ij} = number of observed cases categorized in the i th row of the j th column (Siegel and Castellan, 1988, p. 191)

Dry weight represents the weight of a living specimen out of water, while wet weight is its weight in water. Body mass (wet weight) is an important factor influencing buoyancy (static or

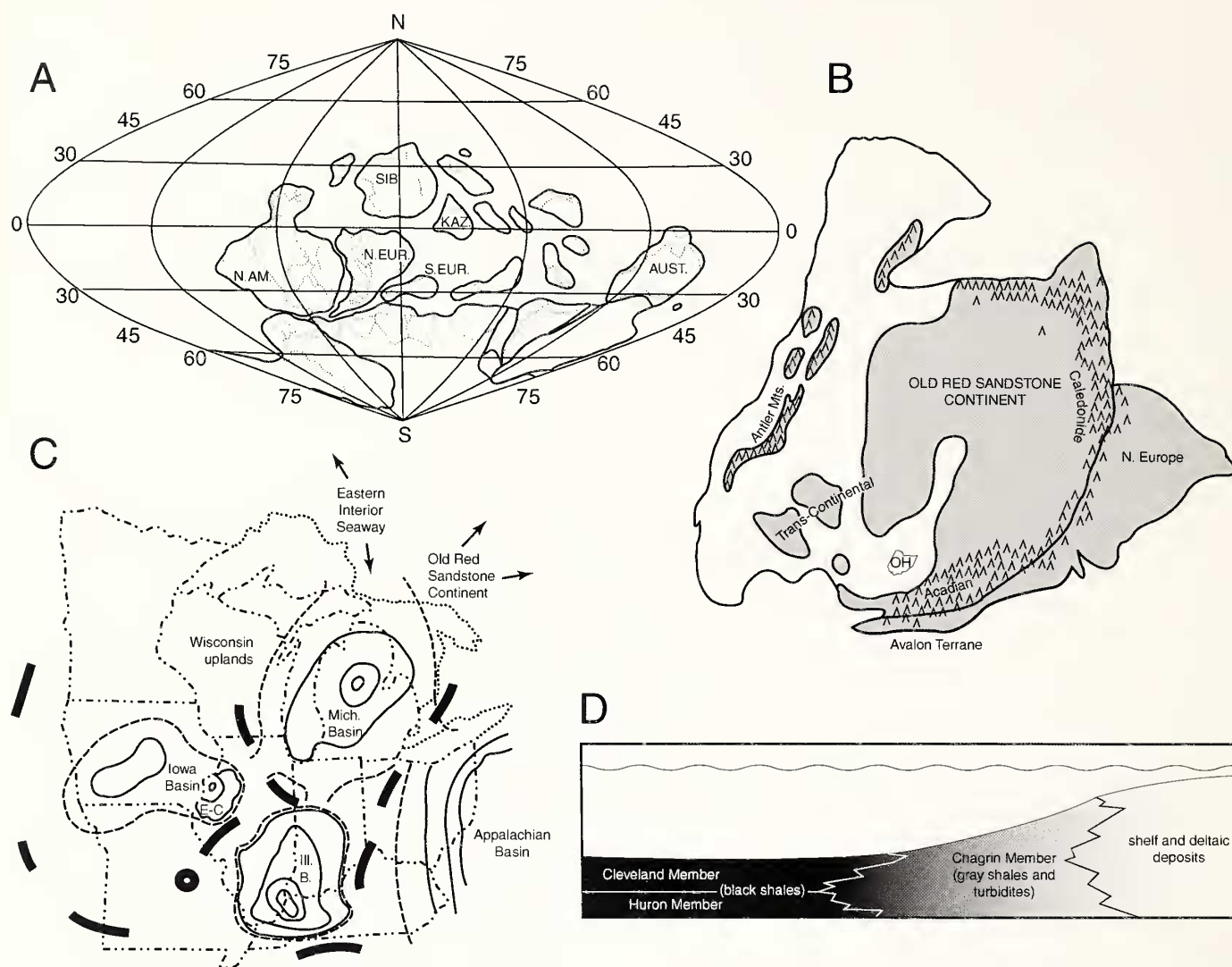


Figure 1. A, paleogeographic reconstruction with paleolatitudes based on Middle Devonian map of Streeel et al., 2000. B, detailed reconstruction of North American and northern European blocks after Ettensohn (1985, fig. 2). The position of Ohio (OH) is indicated and probable landmasses are shaded (A = mountains). C, close-up of the western Appalachian Basin in Ohio and other regional basins (from Elliot et al., 2000, fig. 2). States (dash, double-dotted lines), Great Lakes' boundaries (dotted lines), basin depositional contours (solid thin lines), hypothesized basin boundaries (dashed lines), and regional geographic highs (solid thick lines) are indicated. D, schematic cross-section of the Ohio Shale (Cleveland and Huron Members) and the laterally equivalent shoreward (eastward) sediments.

dynamic) in active swimmers, equally important to benthic forms when considering an unstable substrate, and an important consideration in the post-mortem transport of carcasses. To evaluate locomotor patterns in *Dunkleosteus terrelli*, estimates of its wet and dry weight were calculated based on a conservative comparison to extant Western Atlantic sharks and ten Pacific examples for three species with limited or no Atlantic weight data. A total of 59 length-weight examples from 18 species were used (Bigelow and Schroeder, 1948, all of their reported length-weights were included in this analysis). Bigelow and Schroeder (1948) provided a conversion factor for dry to wet weight in sharks (5.5% for noncontinuous and 2.6% for continuous swimmers) that was applied to *Dunkleosteus terrelli*. The lack of bone in sharks gives a conservative estimate for dry and wet weight in *D. terrelli*; however, the purpose of this estimate was to evaluate its impact

on potential settling in bottom sediments and buoyancy (static or dynamic).

After Allison et al. (1995, p. 98), the root *aerobic* is used here to refer to "modes of life or biofaces," while *oxic* refers to oxygen levels within the environment. The specimen-number prefix CMNH denotes specimens from the Cleveland Museum of Natural History Department of Vertebrate Paleontology.

Results

The raw data of specimens with or without gnathal plates are summarized in an $r \times k$ contingency table (Table 1). A Chi-squared analysis for the five independent samples gives a Chi-square of 6.1 with four degrees of freedom. The critical Chi-square value for $\alpha = 0.05$ is 9.49, thus the null hypothesis (H_0)

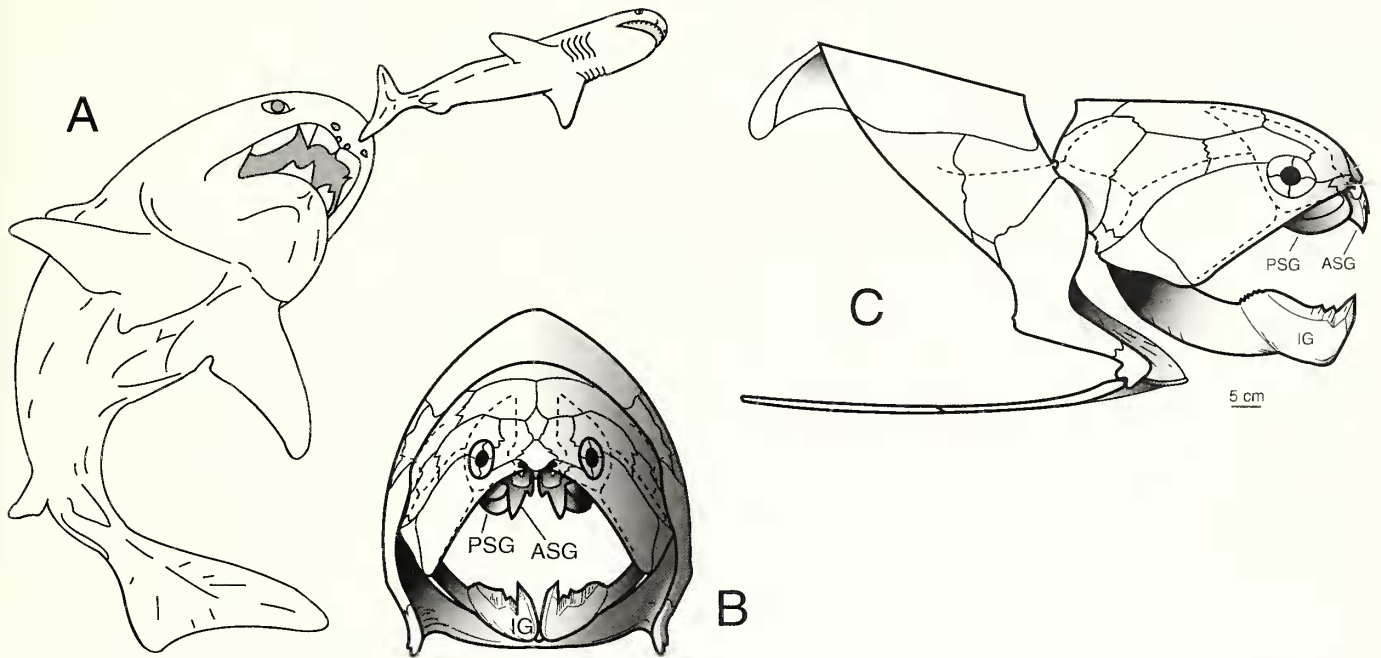


Figure 2. A, life reconstruction of *Dunkleosteus terrelli* in pursuit of *Cladosepiche*. Redrawn from Carr (1995, fig. 17). B and C, anterior and right lateral views of *D. terrelli* ossified skeleton (composite after Heintz, 1932 and 1968). ASG = anterior superognathal, IG = inferognathal, PSG = posterior superognathal, dashed lines = sensory canal grooves.

is not rejected ($0.10 < P < 0.20$). An analysis of three samples (transects 1, 3, and 5, thus eliminating any potential geographic overlap of adjacent transects) does not lead to a rejection of the null hypothesis ($X^2 = 0.64$, d.f. = 2; $0.70 < P < 0.80$).

The log of dry weights versus log of body length for 59 extant sharks (taken from Bigelow and Schroeder, 1948) provided an estimated dry weight for *Dunkleosteus terrelli* (Figure 4). Dry weight for a 4.6 m (15 ft) *Dunkleosteus terrelli* is estimated at 665.0 kg (1466.3 lbs). A wet weight estimate is 36.6 kg (80.6 lbs; or using a continuous swimmer conversion factor, 17.3 kg (38.1 lbs)).

Discussion

Given the precautions concerning interpreting paleoecology based on a fragmentary fossil record (e.g., Elder, 1985; Elder and Smith, 1988; Allison et al., 1991), it is important to evaluate all available evidence. Elder and Smith (1988) presented a method to interpret fish ecology from taphonomic evidence. Using principles of information theory (Tasch, 1965) in their studies of fish taphonomy within lakes, they noted that taphonomic processes provide an informational trade-off. As information about an organism is lost during the taphonomic process, these processes themselves provide new information about the organism's physical and chemical environment and the post-mortem history of the organism. Taphonomy provides not only information on the environment of burial, but if explored fully, the post-mortem history may reveal details about the source of these organisms and their life habitat. Unlike a laboratory experiment where individual variables can be controlled, historical events require a thorough consideration of all taphonomic variables.

The fossil record for placoderms is meager, limiting evaluation of habitat and life history. Within the Appalachian Basin, *Dunkleosteus terrelli* is numerically the predominant Late

Devonian vertebrate fossil. It is one of the best-described members of the fauna (Heintz, 1932) and is recognized easily due to its large size and distinctive osteology relative to the other large members of the fauna (e.g., the thin plates and unique morphology of *Titanichthys* clearly distinguish this taxon from *Dunkleosteus* within the Cleveland Member fauna). *Dunkleosteus terrelli* specimens range in estimated size from 25 cm to 6 m with some even smaller specimens questionably attributed to the species. This size range represents a wide range of age classes.

The available *Dunkleosteus terrelli* material housed within the Cleveland Museum of Natural History was collected over many decades. Peter A. Bungart (Hlavin, 1976) collected, from 1923 to 1946, the bulk of the material in the region of Cuyahoga and Lorain Counties in northern Ohio (Figure 3), diligently and meticulously recording all material associated with a single individual even when collecting continued over several years. This collection possibly represents the best Paleozoic material amenable to statistical analysis with the least amount of sampling bias.

Although questions remain concerning the origin of anoxic basins (Hoover, 1960, p. 31; Degens et al., 1986; Wignall, 1994; Schieber, 1998), a number of factors are common to the various hypotheses relating to the development of black shales such as the Cleveland Member, including: (1) minimal or lack of available oxygen (Hoover, 1960; Heckel, 1972; Degens and Ross, 1974; Brumsack and Thurow, 1986; Wignall, 1994; Allison et al., 1995); (2) presence of hydrogen sulfide representing a potential toxin (Hoover, 1960, p. 34; Heckel, 1972; Jannasch et al., 1974); (3) an unstable substrate consisting of fine sediments with high porosity (Keller, 1974); (4) water depths with low light or below the photic-zone (additionally, below wave base), and (5) limited or lack of trace fossils and bioturbation (bioturbation in the Cleveland Member is reported by Lewis, 1988, p. 25; Schieber, 2003, notes

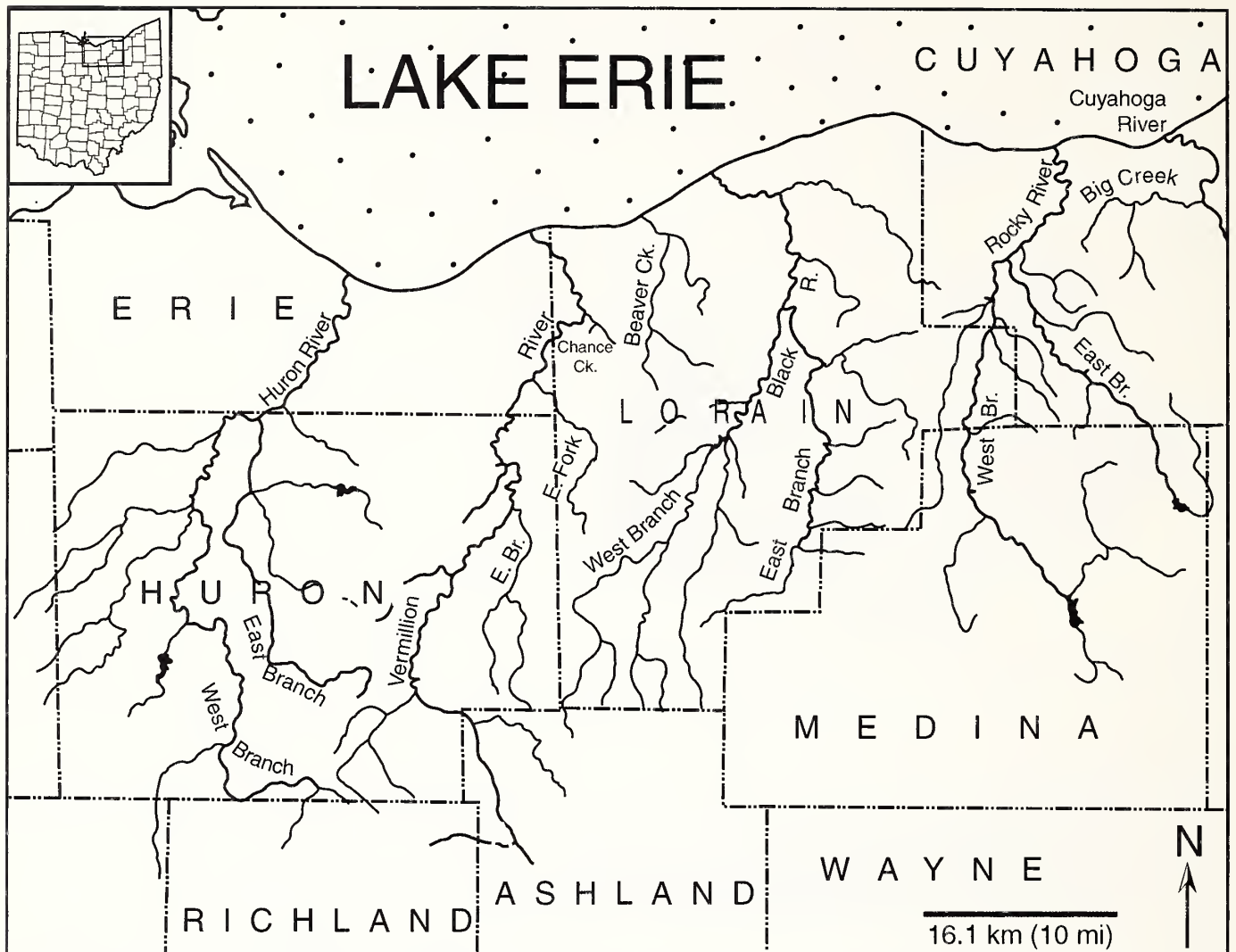


Figure 3. Drainage map of northern Ohio showing the seven river or creek drainages that provided specimens in the current study. Inset map of Ohio indicates the study area (box). Labels: counties, intermediate sized font; and creeks/streams, small sized font. Compiled from Ohio Department of Natural Resources, Principal streams and their drainage areas (map), 1985, and U.S. Geological Survey Kipton, Ohio, 7.5-minute quadrangle topographic map, 1969.

the unrecognized presence of bioturbation in black shales; see Brett and Allison, 1998, for a review of paleontological approaches to interpreting the environment of deposition). The combined effects of the first four factors above clearly impact the potential for the establishment of a benthic community. Common to all models are anoxic pore waters (factor 1). What differs is whether anoxia extends from the sediment-water interface up into the water column. Published accounts of the benthic community associated with black shales (factor 5) range from a complete absence of benthic organisms (Hoover, 1960, p. 32, 42; Conant and Swanson, 1961, p. 56–62; Heckel, 1972; Hlavin, 1976; Allison et al., 1995, p. 100) to low diversity communities capable of tolerating the physical properties of the depositional environment (anoxic-dysoxic, stable or intermittent; hydrogen sulfide; depths potentially below the photic-zone; and unstable substrate; Hannibal et al., 2005). Detailed geochemical (e.g., degree of pyritization) and published sedimentological data for the Cleveland Member are limited, although recent studies of laterally

equivalent black shales, other non-contemporaneous black shales, or modern examples provide useful analogues for the Cleveland Member (hopefully similar studies will be expanded to include the Cleveland Member).

Modern oxygen-minimum zones that intersect the sediment-water interface are known from numerous regions of high primary productivity, for example, the northwest Indian Ocean (Degens et al., 1986) and the Gulf of California (Brumsack and Thurow, 1986). However, there are only a few examples of potential analogues for stagnant foreland basins, including the Black Sea (Degens and Ross, 1974) and Norwegian fjords (Brumsack and Thurow, 1986). The Black Sea, a potential modern analogue to the ancient distal Appalachian Basin, is characterized by a reduced sedimentation rate (variable within the basin) and high sediment porosity with the sediments containing greater than or equal to 71% water by volume (Keller, 1974). Sedimentation occurs within an anoxic water column with toxic levels of hydrogen sulfide. The upper few millimeters of sediment

Table 1. Contingency tables ($r \times k$) for the *Dunkleosteus terrelli* specimens in the current study. Table for five river/creek drainage basins represents north-south transects paralleling the ancient Catskill shoreline. The critical χ^2 value for alpha = 0.05 is 9.49; therefore, the null hypothesis is not rejected ($0.10 < P < 0.20$). Table for three samples (drainage basins) eliminates any potential geographic overlap of adjacent transects. The critical χ^2 value for alpha = 0.05 is 5.99; therefore, the null hypothesis is not rejected ($0.70 < P < 0.80$). Calculations based on Equation 1. Abbreviations: *df*, degrees of freedom [$(r - 1)(k - 1)$]; E, calculated expected occurrences; O, observed occurrences; 1, Huron and Vermilion Rivers and Chance Creek; 2, Beaver Creek; 3, Black River; 4, Rocky River; and 5, Big Creek and Interstate-71.

Contingency table for five drainage basins											
Gnathals	1-O	1-E	2-O	2-E	3-O	3-E	4-O	4-E	5-O	5-E	Total
With	18	17.48	4	3.35	7	7.44	13	8.18	32	37.56	74
Without	29	29.52	5	5.65	13	12.56	9	13.82	69	63.44	125
Total	47	47.00	9	9.00	20	20.00	22	22.00	101	101.00	$N = 199$
O^2/E	18.54		4.78		6.59		20.66		27.26		
	28.49		4.42		13.45		5.86		75.04		
Σ	205.10										
$\chi^2 = \Sigma - N$	6.10										
<i>df</i>	4										
P value	0.1 < P < 0.2										
Contingency table for three drainage basins											
With	18	15.95			7	6.8			32	34.27	57
Without	29	31.05			13	20.66			69	66.73	111
Total	47	47			20	20			101	101.00	$N = 168$
O^2/E	20.32				7.22				29.88		
	27.08				12.78				71.34		
Σ	168.64										
$\chi^2 = \Sigma - N$	0.64										
<i>df</i>	2										
P value	0.7 < P < 0.8										

are unable to support even the remains of microorganisms. The next 30–60 cm are reported to have the consistency of a “slurry” (Keller, 1974, p. 333). Shear strength does not improve within the sediments until a depth of approximately 140 cm (Keller, 1974, fig. 2). Associated with the anoxic water column and presence of hydrogen sulfide is the formation and accumulation of iron sulfides (Bernier, 1974; Rozanov et al., 1974). Neither the Black Sea or fjords (episutural basin of extreme depth or drowned glacial valley with restricted surface area, respectively) are truly representative of the large epicontinental basins of the Devonian; however, the muds deposited in these anoxic environments share the physical properties of sediments that potentially form black shales.

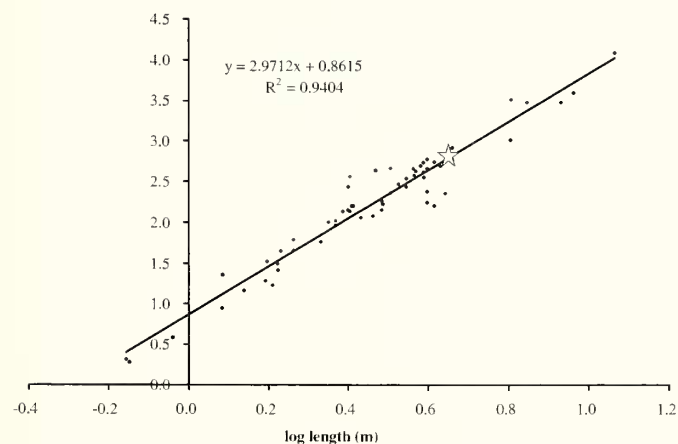


Figure 4. Plot of log dry weight versus log body length for extant North Atlantic sharks (circles). Estimated dry weight for *Dunkleosteus terrelli* of 665.0 kg (1466.3 lbs) for a body length of 4.6 m (15 ft) is indicated by a star.

The Cleveland Member (Nelson, 1955; Hoover, 1960; Mausser, 1982) is typical of black shales with a high organic content accumulated in an anoxic environment. The shale produces a petroliferous odor when freshly broken due to this organic content (Hoover, 1960, p. 23). Its composition of fine sediments, with little or no carbonates in the bulk of the shale (Mausser, 1982, p. 86; although discontinuous cone-in-cone and carbonate concretions are present), suggests an unstable high-porosity substrate at the time of deposition (estimated water content at the time of deposition for the Cleveland Member is 75–80%, J. Schieber, personal communication, 2004). The presence of disseminated pyrite (Mausser, 1982) throughout the formation indicates the presence of hydrogen sulfide at the time of deposition.

In northern Ohio, Upper Devonian Appalachian Basin rocks are exposed in a number of north-south river basins that drain into Lake Erie (Figure 3). These river basins represent a series of north-south transects that roughly parallel the ancient Catskill Delta (Figure 1B, C) thereby providing a series of proximal-to-distal samples within the black shales of the Appalachian Basin. The Cleveland Member represents the distal element of the basin facies that are laterally equivalent to the eastward slope deposits of the Chagrin Member (Figure 1D). This shoreward facies transition is a temporally repeated pattern within the Appalachian Basin as noted by Baird and Brett (1986) for the Genesee sequence of New York.

Evaluation of the paleogeographic distribution of *Dunkleosteus terrelli* provides two potential hypotheses: (H1) *D. terrelli* lived, died, and was preserved within the basin; (H2) *D. terrelli* lived and died elsewhere, but was transported into the basin where it was preserved. The paleogeography of *D. terrelli* is reflected in the nature and distribution of its remains within the Cleveland Member. Hypothesis 1 would suggest the possibility that remains of this species are either intact (no disarticulation due to post-

mortem transport or through other processes) or disarticulated (if disarticulated in transport then there should be no pattern suggesting an eastward source of remains from outside the deep basin). Hypothesis 2 requires transport of *D. terrelli* remains into the deep basin. Associated with the latter hypothesis would be a pattern reflecting the distance traveled from the source (e.g., more complete specimens proportionally found closer to the source or elements that disarticulate early in the taphonomic process found closer to the source).

The remains of *Dunkleosteus terrelli* within the Cleveland Member are typically disarticulated with a variable number of plates missing (only 5.1% of the evaluated specimens possess over 25% of the dermal and perichondral bones). Elder (1985) and Elder and Smith (1988) noted three potential sources for the disarticulation and removal of organic remains in an aquatic environment: flotation, scavenging, or transport by currents (see also Allison et al., 1991). Within the distal Appalachian Basin, the latter two mechanisms have little or no influence on organic remains once they have settled to the bottom. Proposed mechanisms to account for anoxia and the deposition of black shales require an environment below wave base that may be further restricted from mixing by the presence of a density stratification (formation of a pycnocline; see Murphy et al., 2000, and Sageman et al., 2003, for alternative models for the formation of an anaerobic benthos). An anoxic environment (and presence of hydrogen sulfide in some models) would make the bottom unsuitable for macroscopic scavengers; however, that does not preclude scavenging upon floating carcasses within the water column. The presence of an unsuitable bottom habitat is supported in part by the limited or lack of bioturbation and trace fossils. Additionally there is little evidence for the presence of a diverse macroscopic infauna or epifauna, and no evidence for the presence of epibionts encrusting bones. Fossil sharks within the Cleveland Member often are found fully articulated with soft tissues preserved (Williams, 1990). These fossils have been reported from carbonate concretion zones in the shales of Big Creek and Interstate-71. This represents a sampling bias in that concretions are easily seen in profile, in contrast to flattened isolated specimens. Shark fossils are found from outside the concretion zones in westward deposits either associated with cone-in-cone deposits or isolated within the shale. The skeletons of these fishes consist of perichondrally ossified prismatic cartilage that is highly susceptible to mechanical damage and is destroyed easily by scavengers or currents.

The fine grain size of Cleveland Member sediments further suggests a relatively low energy depositional environment (Nelson, 1955; Mausser, 1982) and the absence of currents sufficient to move the relatively large bones of *Dunkleosteus terrelli*. Additionally, there are no sedimentary structures (bedding features) suggesting the presence of higher energy bottom currents within the Cleveland Member. Sediment winnowing does occur, demonstrated by the presence of several isolated lag deposits (invertebrate thanatocoenoses, Hlavin, 1976; silty lags, J. Schieber, personal communication, 2004); however, winnowing tends to accumulate bone and pelagic invertebrates rather than remove them. The large and relatively heavy *Dunkleosteus terrelli* bones would preferentially remain within these deposits.

Flotation remains as the most plausible mechanism to account for the disarticulated remains of *Dunkleosteus terrelli*. Flotation could occur in fishes living within the basin or it may represent a mechanism for the transport of organisms into the basin.

Common to the patterns of disarticulation in both aquatic (Elder, 1985; Schäfer, 1972) and terrestrial (Hill, 1979; Weigelt, 1989) organisms is the loss of elements near sites of access by scavengers (microscopic and macroscopic). The oropharyngeal cavity represents such a site with scavenging activity in this region resulting in the disarticulation and potential loss of gnathal elements. In teleosts and arthrodires (Figure 2B, C) both upper and lower gnathal elements, which lack ossified connections to the axial skeleton, are lost. In contrast, within mammals where the maxillae and premaxillae are connected intimately with the skull, the dentaries alone are detached from the skull. Work by Elder (1985) and others (Schäfer, 1972; Hill, 1979; Smith and Elder, 1985; Elder and Smith, 1988) suggests that gnathal elements (dentaries only in mammals) in particular are lost early in the disarticulation process, thus presence of specimens with gnathal elements suggests a relatively short time of exposure to pre-burial taphonomic processes (including both transport and scavenging). In the case of *Dunkleosteus terrelli* within the Appalachian Basin, the presence of isolated gnathal plates suggests that floating carcasses may have dropped elements relatively close to the original life habitat.

Elder (1985), Smith and Elder (1985), and Elder and Smith (1988) documented the importance of water depth and temperature to the process of flotation. The physical principles outlined in the gas laws of Charles and Gay-Lussac ($k = VT$) and Boyle ($k = PV$) clearly delineate limitations for the potential of an organism to float upon bacterial decomposition within finite ranges of water depth and temperature. Thus, the volume of accumulating decomposition gases within the tissues or body cavities to induce flotation will increase with warming (a latitudinal or climate factor) and decrease with depth (increased pressure). Elder (1985) suggested a limiting depth for flotation in a number of teleosts although her experimental work did not consider larger species or variable densities. She suggested that settling below a depth of 10 m even within tropical waters would severely limit or prevent flotation. In contrast, Allison et al. (1991) noted the calculated potential of flotation in whales up to a depth of 1200 m. Unlike the teleosts studied by Elder (1985), whale specimens may be nearly neutrally buoyant at the time of their settling to the bottom (some are positively buoyant and float at the time of death, representing an inherent static buoyancy, Allison et al., 1991).

The Appalachian Basin in the Late Devonian was located in the subtropics (30–35° S), suggesting moderate to warm water temperatures (17–18° C) based on oxygen isotopic data from brachiopods (Streel et al., 2000, fig. 30, p. 154). Several authors dispute the water depth within the open Appalachian Basin; however, all estimates are well within the computed depths of Allison et al. (1991) that are necessary for flotation (61.0–91.4 m, Nelson (1955); 30.5–45.7 m, Hlavin (1976); 50–100 m, Brett et al. (2003); up to 100 m using the depth limits, noted by Ferguson (1963), for *Lingula* found within the Cleveland Member; contrast these estimates with Schieber's (1998) estimate of 10–20 m for the Chattanooga Shale of Tennessee, although, the Chattanooga Shale is characterized by a number of lag deposits and erosional surfaces).

The presence of *Dunkleosteus terrelli* remains in the black shales of the Appalachian Basin can be explained either as a post-mortem accumulation of organisms that lived within the basin or a rain of parts falling from carcasses transported via flotation from aerated regions. The results of a Chi-squared statistical analysis of these fossils did not support the hypothesis that *D.*

terrelli was restricted to the shallow aerated eastern part of the basin and that its presence in the distal sediments was the result of carcasses floating into the basin (Table 1; $\chi^2 = 6.1$, d.f. = 4, $0.10 < P < 0.20$). In an additional analysis of non-adjacent transects (nos. 1, 3, and 5), the null hypothesis was not rejected ($\chi^2 = 0.64$, d.f. = 2, $0.70 < P < 0.80$). Non-rejection of the null hypothesis is consistent with a random distribution of *D. terrelli* within the basin, thus it is more likely that this species was a pelagic form (living and dying within the basin) and not an obligate bottom dweller (restricted to the eastern aerated shallower benthos, e.g., the basin slope represented by the Chagrin Member or more shoreward regions, Figure 1D).

Given our knowledge of the bottom habitat associated with black-shale formation, *Dunkleosteus terrelli* would have had to be a continuous swimmer. The paleontological, sedimentological, and geochemical evidence all suggest that the bottom environment was inhospitable; however, even if fishes could reach the bottom within the basin, the stability of the substrate to support the weight of these organisms would have proven to be a problem.

At present there are few estimates for the size or weight of *Dunkleosteus terrelli* (Heintz, 1932). The large amount of bone and concomitantly high body mass has led several researchers to conclude that *D. terrelli* must be a benthic form (e.g., Denison, 1978; although rejected by later authors, Heintz, 1932, considered *Dunkleosteus* to be an active swimmer and predator). Comparison of *Dunkleosteus terrelli* (using an adult length of 4.6 m (15 ft) to modern sharks (Figure 4) suggests a dry weight of approximately 665.0 kg (1466.3 lbs). Bigelow and Schroeder (1948) suggested that wet weight is 5.5% of dry weight in extant sharks (2.6% for free or continuous swimming forms). Using this estimate, the wet weight for *D. terrelli* can be calculated to be 36.6 kg (80.6 lbs; or using a free swimming estimate, 17.3 kg or 38.1 lbs). This represents a conservative estimate due to the lack of bone in sharks and the conversion to wet weight being based on organisms possessing lipids for static buoyancy. A wet weight of 36.6 kg (or 17.3 kg for continuous swimmers) would generate sufficient shear forces to permit the settling of *D. terrelli* into the substrate exposing it to the toxic properties of the sediments and potentially clogging the gills with fine silt (refer to Keller, 1974, p. 333–334, for estimates of shear strength in black muds). If *D. terrelli* lived within the basin it can be assumed that it did not rest on the bottom, but swam continuously.

A second point bearing upon the interpretation of placoderm lifestyles is their mode of locomotion. Placoderms apparently possessed a low profile and poorly supported heterocercal tail and have been interpreted to have swum using a sine-wave undulation of the body (Thomson, 1971; anguilliform locomotion of Lindsey, 1978). They have been compared to extant macrurid or chimaerid fishes (Stensiö, 1963, p. 13), which demonstrate a bottom-dwelling lifestyle. Although anguilliform locomotion may be considered a relatively inefficient form of locomotion (e.g., relative velocity between anguilliform and other forms of locomotion) it does not mean that anguilliform swimmers are not effective prolonged or continuous swimmers. One needs only to look at the migratory patterns of extant eels (*Anguilla anguilla*), which migrate between North America and Europe (McDowall, 1988) to recognize this point. Although placoderms apparently never achieved some of the advanced forms of locomotion seen in modern teleosts (e.g., carangiform and thunniform locomotion, Lindsey, 1978), they did develop a number of locomotor adaptations associated with increased lift and reduced drag (Carr, 1995).

Conclusion

The taphonomic evidence did not support an interpretation of *Dunkleosteus terrelli* as an obligate benthic organism. A Chi-squared statistical analysis of the distribution for the remains of this species failed to support a restricted bottom-living hypothesis. *Dunkleosteus terrelli* was a free-swimming species living within the Appalachian Basin, which may help to explain its wide North American distribution (California to eastern United States; if synonymised with *D. marsaisi* (Lehman, 1954) from Morocco (Rücklin, 2002) the range would extend via the Rheic Ocean to east of the Old Red Sandstone Continent, Figure 1A). This interpretation is consistent with the analysis of Carr (1995), which noted the development of locomotor specializations within pachyosteorhynchid arthrodirans and was further supported by the preservation of relatively complete specimens or the distribution of elements lost early in the disarticulation process throughout the basin.

Potential objections to viewing placoderms as free-swimming organisms have included their possession of heavy body armor and an anguilliform form of locomotion. The distribution of *Dunkleosteus terrelli* remains in the Appalachian Basin is consistent with disarticulation due to localized post-mortem flotation. The presence of post-mortem flotation in a basin with published depth estimates ranging from 30 to 100 meters suggests an organism with some level of additional static buoyancy beyond inherent tissue buoyancy (refer to Allison et al., 1991). An interpretation of anguilliform locomotion does not necessarily imply an ineffective form of locomotion. It appears that an interpretation of bottom life is a consequence of the researcher's choice of extant analogue rather than any necessary correlation between lifestyle and form of locomotion.

The implications of this study are three-fold and form the basis of continuing work on the Cleveland Member fauna. Life within the basin raises questions concerning the: (1) reproductive strategy; (2) life history; and (3) static buoyancy in *Dunkleosteus terrelli*. An inhospitable bottom limits potential nesting sites. It is not possible at this time to determine whether this species was viviparous or oviparous; although, the presence of putative egg cases within the Cleveland Museum of Natural History collections (CMNH 8133–8136, 9461) raises some interesting questions. Further work is needed to provide information on the distribution of age classes for *D. terrelli* within the Appalachian Basin. Finally, the presence of disarticulation associated with flotation raises questions concerning static buoyancy in *D. terrelli*. Elder (1985) has pointed out the physical limits (depth and temperature) associated with flotation; however, Allison et al. (1991) have demonstrated that given sufficient static buoyancy, flotation may occur up to depths of 1200 m. The presence of air sacs in placoderms has been questioned (Denison, 1941, recognized the presence of air sacs in *Bothriolepis*, but did not consider them to be a feature of placoderms in general, although this interpretation has never been confirmed in other specimens of *Bothriolepis* or in any other placoderm taxa (D. Goujet, personal communication, 2004); Gardiner, 1984, considered air sacs to be a derived feature within Osteichthyes). However, the predominance of disarticulation associated with floating in *D. terrelli* strongly suggests the presence of a static buoyancy mechanism within this species (if not an air sac then potentially lipids as seen in chondrichthyans). Further work on taphonomic patterns and flotation within *D. terrelli* may help to shed light on these questions.

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